WIND-SHELTERS AS SAFE SITES FOR ESTABLISHMENT OF *LUPINUS ARBOREUS*, A COASTAL SPECIES

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Abstract

To learn the effect of wind on a species native to a windy site, I compared germination, seedling survival, seedling form, and the force required to uproot seedlings in a wind-exposed and a wind-sheltered site. In February 1992, the sand dune perennial *Lupinus arboreus* Sims. was planted in wind-exposed and wind-sheltered plots at Bodega Head, California. Half the individuals were planted from seed and the other half were transplanted from nearby. By late July 1992, 26/43 of the germinants or transplants were still alive in the wind-protected plot but only 3/42 in the wind-exposed plot. This suggests the importance of wind-sheltered sites as safe sites for establishment of this dune species. By 57 days after planting the average plant was smaller in the wind-exposed than the wind-swept plot (P < 0.05), but those seedlings that would survive until harvest (day 151) were significantly larger in both plots than those that would die (P < 0.05). These data suggest that rapid early growth was important to survival. The wind-exposed survivors at day 151 (n = 4) tended to have morphologies more resistant to wind: they averaged twice the stem diameter (2 cm above the ground) and half the height of wind-protected plants (n = 28). There were no significant differences in the force required to uproot plants by treatment (P < 0.05). Two non-native lupines were also planted from seed to learn how congeners respond to wind. Germination, establishment, and growth of *L. cosentinii* Guss. plants were unaffected by wind, perhaps because the large seed permits rapid development of a taproot to aid in water acquisition. Seedlings of *L. angustifolius* L. cv. Ganja died quickly after total defoliation by caterpillars, suggestive of a major role of chemical defenses for survival of lupines at this sand dune site.

Wind contributes to many aspects of plant form and demography, including growth form, survival, physiology, and dispersal of propagules (Nobel 1981). After asking the effect of simulated wind on the form of tomato plants in a greenhouse (Gartner 1994), I wanted to learn how wind affects the survival, form, and biomechanical function of an undomesticated plant in its native windy habitat.

In response to wind or mechanical stimulation such as rubbing, shaking, or flexing, most plants develop a compact form, with shorter internodes and petioles, and sometimes shorter, thicker, darker epinastic foliage (reviewed in Mitchell et al. 1975; Grace 1977; Jaffe

1980; and Biddington 1986). Heiligmann and Schneider (1975) found higher root/shoot dry weight ratios in wind-exposed than wind-protected seedlings of black walnut (*Juglans nigra* L.). Several studies have shown that wind increases allocation to roots, which has been interpreted as a means of increasing a plant's capacity to supply water to the shoot for transpiration (Biddington and Dearman 1985); yet increased root allocation could also result from a shift toward more allocation for anchorage. An optimal plant design to resist lateral forces (such as those induced by wind), is possession of large rigid members near the soil surface (Ennos and Fitter 1992). These rigid members can be a taproot, upper lateral roots, rhizomes, or bases of stems. The response of tomato plants to simulated wind is consistent with Ennos and Fitter's model: increased diameter of the lower stem and upper taproot (Gartner 1994). The taxa in the current study were also taprooted, and I expected to find morphological changes in them similar to those in tomato plants when grown in a wind-exposed habitat compared to a wind-sheltered one.

The current project was undertaken at Bodega Head in northern California, a site with daily strong afternoon winds during late spring and summer. This site was ideal because of its windiness, its abundant *Lupinus arboreus* Sims. (yellow bush lupine), its biological station for weather information and logistical support, and its protection from beach-goers. I chose the species because it is woody (living to a maximum of about 7 years, Davidson and Barbour 1977), thus not switching entirely to a strategy of reproduction at the end of a growing season. Also, it is native to very windy sites, grows well on sand, has an upright form that will catch the wind, and has a non-clonal growth form (Davidson 1975). I also studied two agronomic lupines, *L. cosentinii* Guss. and *L. angustifolius* L., to determine if these plants have the same reaction to wind as the native species.

My hypotheses were 1) that lupines grown in a wind-exposed plot have lower survival than those in the wind-protected site; and 2) that plants in the wind develop shorter, wider stems, and wider taproots than plants in the wind-protected site, and that the force required to uproot the wind-exposed plants exceeds that required to uproot the wind-protected ones. Thus, I expected that plants in windy sites have a form conferring some resistance to overturning by wind, but that they nonetheless would exhibit decreased survival.

Materials and Methods

Site. Plants were studied at Bodega Head, in north-central California (latitude 38°18′N, 123°04′W), on the grounds of the University of California Bodega Marine Reserve. Experiments were undertaken during 1992 in a stabilized dune area, with grasses and lupines covering much of the vicinity. The plots were installed on

sparcely vegetated areas that were underlain with many, many roots. The predominant winds blow from the north–northwest, as indicated by the orientation of the dunes. The plots were 400 m downwind from the shore, with their leading edge perpendicular to the predominant winds.

Bodega Head is a windy location. From mid-April to mid-June the mean maximum daily wind-gust velocity was 119 m/sec (1988–1992, measured for 4-second gusts). The July 1991–June 1992 year had about average rainfall (67 cm vs. 74 cm for the 23-year average), although rainfall during the period of seedling establishment was higher than average (39 cm for Feb.–June 1992 vs. 28 cm for that same period in the 23-year average).

Plots. I installed two 7 × 11 m plots, designating the upwind one as wind-exposed and the downwind one (10 m away) as wind-protected. Each plot was surrounded by a 1.8 m high chicken-wire fence (5 cm mesh) designed to exclude rabbits and deer. The base of the fence was buried 10 cm in the sand. The wind-protected plot was then covered with clear plastic sheeting on the leading edge (to a height of 1.8 m) and the right and left sides (to heights of 1.4 m), forming a large U (Fig. 1). To further reduce air motion in the plot, I installed three plastic-covered fences (1 m tall) parallel to the plot's leading edge.

I used a hand-held anemometer (Dwyer Instrument Co., Michigan City, IN) to spot-check windspeeds in the two plots. I recorded the maximum windspeeds on three occasions in 54–78 locations/plot (5-sec periods 20 cm above the ground) and alternated from one plot to the other after each set of four measurements. These measurements were intended to indicate the relative windiness of the two plots, not to quantify the wind itself. Measurements were taken mid-day on 27 May, 7 June, and 30 July. On 20 July, I took five samples of sand from the top 5 cm of each plot for determination of particle-size distribution (using the hydrometer method, Gee and Bauder 1986) and electrical conductivity (using an aqueous substrate paste, Rhoades 1982). Electrical conductivity is an indicator of the substrate's salinity.

The wind-protected plot was less windy than the exposed plot at all times tested (Table 1). The magnitude of wind reduction by the barriers differed by date, probably due to different wind directions, wind speed, and possibly duration (gustiness). The soil substrate did not differ significantly between plots, either in particle-size distribution or electrical conductivity (analysis of variance, $P < 0.05$). Both plots were composed of 99.8–99.9% sand (particles >0.05 mm in diameter) on a dry-weight basis. Electrical conductivity averaged 0.23 ± 0.01 mmho/cm in the exposed plot (mean ± SE, n = 5), and 0.28 ± 0.03 mmho/cm in the protected plot. Therefore, the
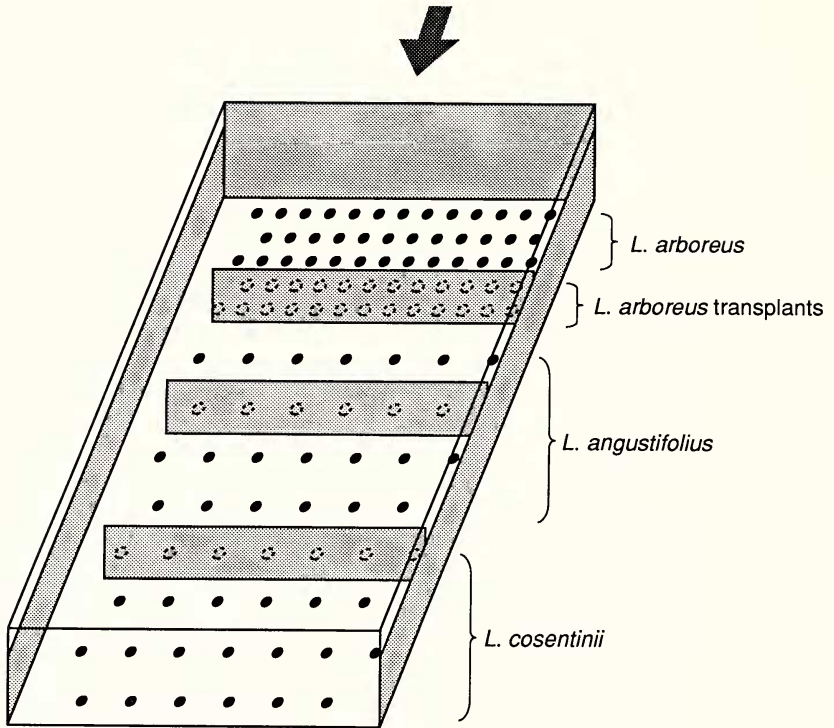
Fig. 1. Diagram of the wind-protected plot showing the predominant wind direction (arrow), 1.8-m tall perimeter fence, plastic barriers (shaded), and locations of seeds or transplants.

plant results I obtained were likely due to the treatments themselves and not to uncontrolled environmental differences.

Cultivation. Lupinus arboreus is a perennial shrub native to dunes and the surrounding vegetation at Bodega Head. The *L. arboreus* seeds were collected from Bodega Head the previous year. Both *L.*

TABLE 1.   MAXIMUM WINDSPEEDS AT MID-DAY IN 5-SECOND PERIODS (M/SEC, MEAN ± SE (n); ANOVA).

	Measure-ments/plot (n)	Wind-protected plot	Wind-exposed plot	P
27 May	78	4.7 ± 0.7	21.2 ± 1.1	<0.01
7 June	54	15.1 ± 1.6	22.9 ± 1.4	<0.01
30 July	78	2.6 ± 0.6	7.7 ± 1.1	<0.01

angustifolius and *L. cosentinii* are annual forage plants. Seeds of *L. angustifolius* were obtained from commercial sources and those of *L. cosentinii* were collected from western Australia the previous year. The *L. angustifolius* I studied is an alkaloid-free cultivar (Ganja). In contrast, *L. cosentinii* and *L. arboreus* have high concentrations of alkaloids (B. Bentley personal communication).

On 19 February 1992, I planted the three lupine species in each plot. The first subplot was planted with 38 *L. arboreus* seeds spaced 0.5 m apart. The next subplot had 25 transplanted *L. arboreus* seedlings spaced 0.5 m apart. Several extra seeds were planted in each plot to use as replacements for ones that died. Transplants were taken on a rainy day from within 100 m of the plot. Their seeds had probably germinated within the past 1–2 weeks. Each transplant had cotyledons plus 0–3 leaves. The next two subplots were planted with 26 *L. angustifolius* or *L. cosentinii* seeds spaced 1 m apart, respectively. On April 17 (day 57) I increased the sample size of seedlings to compensate for mortality by including extra seedlings (without moving them) or transplanting recent germinants into the plot (in the seeded and transplanted plots, respectively). These extra seedlings were not used for survival or mortality studies, but were used for biomass and uprooting characteristics. To help seeds germinate and seedlings establish, I watered plots five times between planting and 5 May (day 75). I weeded the plots periodically to remove the volunteer plants that were not part of the study.

Germination, survival, and growth. Survivors were counted on the following days after seeds and transplants were planted: 20 (germinants but not transplants), 57, 97, 108 (*L. cosentinii* only), and 151 (11 March, 13 April, 27 May, 7 June, and 20 July, respectively). Because seeds continued to germinate beyond day 20, I used data from day 53 to calculate the total number of seeds that had germinated (survivors plus standing dead). On day 57 I recorded stem length and number of leaves for each survivor (defined as a plant with green on at least one leaf).

Harvest and force to uproot. I harvested the *L. arboreus* seedlings between 20 and 23 July, 151–154 days after they were planted. Before harvest, I measured the force required to uproot them with a vertical pull at a constant rate of 0.7 mm/sec. The force was provided by a winch mounted on a sawhorse located directly over the decapitated plant (Gartner 1994). A bias-weave sleeve was slipped over the stump of the plant (and affixed with two cable ties). Because of the weave, the sleeve tightens under tension. The sleeve was attached to a spring-scale that was attached to the winch. As I cranked the winch, I watched the spring scale and noted the maximum force before the plant uprooted.

Next, I measured stem length for each *L. arboreus* seedling, and

then stem and taproot diameter every 2 cm. Shoots were then divided into stem or leaf for oven-dry weight determination. I was unable to harvest the roots for dry weight determination because they extended for many meters and intermingled with roots of other plants.

I harvested *L. cosentinii* seedlings on 7 June, 108 days after they were planted. I measured stem length and stem and taproot diameters as described above, then divided plants into stem, leaf, and reproductive tissues for oven-dry weight determination. No *L. angustifolius* plants survived to the harvest date.

RESULTS

Germination, survival, and growth. Seedling survival was higher in the wind-protected plot than in the wind-exposed plot (circles, Fig. 2), but wind had no effect on total germination of *Lupinus arboreus* or *L. cosentinii* (squares, Fig. 2). The data are plotted with absolute numbers of survivors to emphasize sample sizes, but discussed in terms of percentages of total germinants. The survival of *L. arboreus* in the wind-protected plot was 56%, compared to 12% in the exposed plot (Fig. 2A). The difference in survival between plots was even larger for the transplants (64 vs. 4%, respectively; Fig. 2B). For transplants, the early high mortality in the wind-exposed plot suggests that adjustment after transplantation was less successful at the windy site.

The survival of *L. cosentinii* seedlings was slightly higher in the wind-protected than the wind-exposed plot (38 vs. 24%, respectively; Fig. 2C). *Lupinus angustifolius,* the alkaloid-free cultivar, was entirely defoliated, presumably by the larvae of *Platyprepia virginalis* (Lepidoptera, Arctiidae) that were frequently on this lupine. Germination of *L. angustifolius* was higher in the wind-protected than the wind-exposed plot (Fig. 2D) but there were no survivors in either plot 97 days after planting.

For the following size and survival data, I combined data for plants that were introduced as seed and those that were transplanted because they did not differ in size at day 57 or beyond (P > 0.05, data not shown). Average plant size was lower in the wind-exposed than wind-protected plot at day 57 (Table 2). However, there was much variation in *L. arboreus* plant size, and its size at 57 days was predictive of its survival to 151 days (harvest date). On the average, survivors had twice as many leaves and were twice as tall at 57 days as those that died before the harvest (Table 3).

Harvest and force to uproot. There were no significant effects of treatment (wind-protection vs. wind-exposure) on plant size at harvest for either species (P > 0.05, Table 4). *Lupinus arboreus* tended to be shorter and smaller in the exposed than the protected site, but
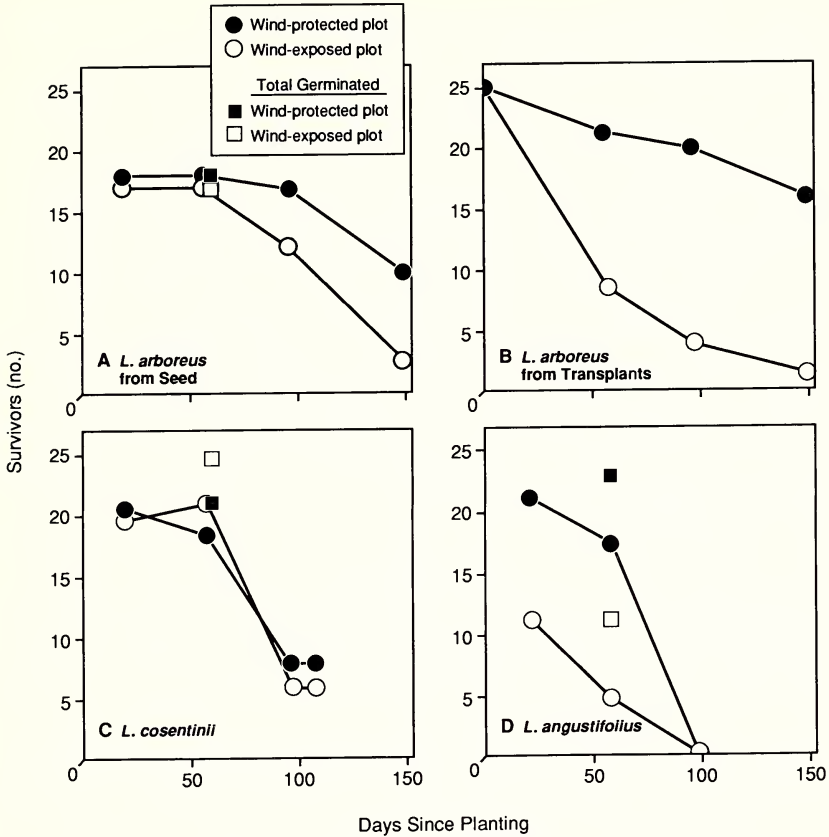
FIG. 2.   The number of *Lupinus* survivors at Bodega Head, California, as a function of species and date (circles) in wind-protected vs. wind-exposed plots. Total germination (including standing dead plus survivors) was determined on day 57 (squares). A) *L. arboreus* planted from seed. B) *L. arboreus* germinants transplanted from nearby. C) *L. cosentinii* planted from seed. D) *L. angustifolius* planted from seed.

this was not significant at $P < 0.05$ (Table 4). Sample sizes in Tables 3 and 4 differ because Table 4 includes the extra seedlings that were used to replace some of those that died.

The force required to uproot a plant was quite variable and was not affected significantly by treatment ($P < 0.05$). On average, however, plants in the wind-exposed plot required only 35% of the force

TABLE 2.   SIZE OF *LUPINUS ARBOREUS*, DAY 57 (MEAN ± SE (n); ANOVA).

	Wind-protected plot	Wind-exposed plot	P
Stem length (cm)	2.0 ± 0.4 (39)	1.0 ± 0.2 (26)	<0.01
Leaves (no.)	6.2 ± 0.7 (39)	2.5 ± 0.4 (26)	0.03

TABLE 3.   SURVIVAL PREDICTION FOR *LUPINUS ARBOREUS*. Length of stems and number of leaves on day 57 for plants that survived until the harvest (day 151) vs. plants that died before the harvest (mean ± SE (n); ANOVA).

	Plants surviving to harvest	Plants dying before harvest	P
Stem length at 57 days (cm)			
Wind-protected plot	2.5 ± 0.4 (26)	1.2 ± 0.6 (13)	0.09
Wind-exposed plot	2.2 ± 0.7 (3)	0.9 ± 0.1 (23)	<0.01
Both plots	2.4 ± 0.4 (29)	1.0 ± 0.2 (36)	<0.01
Leaves at 57 days (no.)			
Wind-protected plot	7.2 ± 0.9 (26)	4.2 ± 0.8 (13)	0.04
Wind-exposed plot	4.7 ± 0.9 (3)	2.2 ± 0.4 (23)	0.06
Both plots	7.0 ± 0.8 (29)	2.9 ± 0.4 (36)	<0.01

of those in the wind-protected plot. Force required to uproot a plant/ stem cross-sectional area at ground level did not differ significantly between treatments (P > 0.05).

DISCUSSION

Protection from wind had no effect on germination but increased seedling survival through the first dry season in *Lupinus arboreus*. Wind-protection increased the number of large plants by day 57 and

TABLE 4.   SIZES OF SEEDLINGS AT HARVEST IN THE WIND-PROTECTED AND WIND-EXPOSED PLOTS, FORCE TO UPROOT THEM, AND RATIO OF PROTECTED TO EXPOSED VALUES FOR *LUPINUS ARBOREUS* AND *L. COSENTINII* (MEAN ± SE; ANOVA).

	Wind-protected plot	Wind-exposed plot	P	Exposed/ protected
Lupinus arboreus	(n = 28)	(n = 4)		
Shoot DW (g)	2.3 ± 0.6	0.2 ± 0.1	0.23	9%
Stem length (cm)	10.7 ± 1.9	5.7 ± 3.3	0.35	53%
Stem or root diameter (mm)				
2 cm above ground	2.2 ± 0.4	3.9 ± 1.1	0.15	177%
At root crown	4.0 ± 0.4	3.1 ± 0.7	0.44	78%
2 cm below ground	3.3 ± 0.4	2.4 ± 0.6	0.40	73%
Force to uproot (kg)	4.0 ± 0.9	1.4 ± 0.4	0.30	35%
Force to uproot/stem cross-sectional area at root crown (g/mm^2)	309 ± 0.46	193 ± 26	0.36	62%
Lupinus cosentinii	(n = 8)	(n = 6)		
Shoot DW (g)	1.2 ± 0.3	1.3 ± 0.4	0.79	108%
Stem length (cm)	11.4 ± 2.2	10.5 ± 1.0	0.74	92%
Stem or root diameter (mm)				
2 cm above ground	3.7 ± 0.6	4.0 ± 0.5	0.67	108%
At root crown	3.5 ± 0.2	3.8 ± 0.5	0.63	109%
2 cm below ground	2.5 ± 0.3	2.7 ± 0.5	0.71	108%

large plants in either treatment were more likely than small plants to survive from day 57 to day 151, indicating that wind-protection promoted rapid early growth which was important for summer survival. These results also suggest that one dimension of a safe site for seedlings (Harper et al. 1961; Fowler 1988) is the mechanical (Patterson 1992) or wind environment. Previous descriptions of safe sites have listed ranges of such factors as temperature, microtopography, light, and chemical composition of the substrate, but have not underscored the importance of shelter from wind. Nonetheless, the role of wind-shelter in boosting establishment of germinants and transplants has long been recognized in agricultural systems (e.g., Salmon 1916; Heiligmann and Schnieder 1975).

Sites protected from wind appear to be safe-sites for seedling survival, but this study cannot name the factor(s) against which the wind-barrier provides protection: mechanical abrasion, salt, desiccation, or developmental exigencies of living with stem motion (the thigmomorphogenetic response). In one study, dune grass establishment was unaffected by wind alone but was greatly hindered by wind-blown sand that ruptured cells, exposing tissues to desiccation, insects, and pathogens (Fryrear et al. 1973). In the current study wind-blown sand was not apparent because the surface of the study area did not change elevation, although saltation could still have occurred. Sea-salt aerosols (e.g., Ogden 1980) or soil-water salinity (e.g., Okusanya 1979; Lee and Ignaciuk 1985) could have caused the higher mortality and lower growth in the wind-exposed than in the wind-sheltered plot. However, growth and distribution data suggest that *L. arboreus* may be relatively insensitive to salt. In a short-term (15-day) study of foliage burn, *L. arboreus* was less sensitive to salt-spray than two species, and shared the same low level of sensitivity as five other species native to the California strand (Holton and Johnson 1979). *Lupinus arboreus* was abundant in three of the six associations at the strand site, occupying dune swales and mesic slopes up to 30 m from the ocean, and some of its microsites received five times the salt deposition as microsites in which other strand species were restricted (Holton and Johnson 1979).

More likely, the wind-barrier boosted establishment by providing a site where more plants could attain a critical size and then reach the water table throughout the dry season. In contrast, in the exposed site, the stunted growth would have increased vulnerability of plants to drought, and plants would ultimately die of drought stress. It is well-established that wind or simulated wind decreases and qualitatively changes the growth of most dicotyledonous and coniferous species (see reviews in Mitchell et al. 1975; Grace 1977; Jaffe 1980; Biddington 1986; and see Patterson 1992 and Gartner 1994), so it is likely that wind decreased *L. arboreus* growth in the more exposed plot. Moisture stress appears to limit *L. arboreus* establishment: an

earlier study on its demography at Bodega Head implicated herbivory, competition with grasses for light and moisture, and low moisture in general as limitations on seedling establishment (Davidson and Barbour 1977).

The first hypothesis, that plants in wind-exposed sites have lower survival than those in wind-sheltered sites, was supported by the data for the two species that had alkaloids in their tissues, *L. arboreus* and *L. cosentinii. Lupinus cosentinii* had low survivorship on both plots and the size of its survivors did not differ significantly by treatment. Even mild water deficits have been shown to decrease net photosynthesis of *L. cosentinii* (Henson et al. 1989). Perhaps the seedlings that were able to become established (regardless of treatment) were those whose taproots reached the water table. Because *L. cosentinii* has larger seeds than does *L. arboreus* (about 220 mg vs. 41 mg/seed, mean of 12 seeds each), seedlings of *L. cosentinii* may have been able to access the water table faster than *L. arboreus,* explaining why wind exposure decreased growth of the *L. arboreus* more than the *L. cosentinii* seedlings.

The alkaloid-free species, *L. angustifolius* was defoliated very soon after germination: there were no live seedlings in either the wind-protected or the wind-exposed site by day 100. The swift disappearance of *L. angustifolius* suggests the effectiveness of chemical defenses in protecting the other lupines from herbivory.

The second hypothesis, that individuals in the wind-exposed plot would have a form more resistant to wind than individuals in the wind-protected plot, was not supported by the data at the significance level $P < 0.05$, although the relative magnitudes of the means for the native species were in the directions predicted by the hypothesis. More survivors are needed to test this hypothesis effectively.

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